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Research Article

The past, present, and future distribution of *Calanthe graciliflora*: implications for conservation and phylogeography

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Abstract

Calanthe graciliflora, an orchid species endemic to China, is one of the most widely distributed members of the genus *Calanthe*, occupying the highest latitudinal range and exhibiting strong cold tolerance. These traits suggest key adaptations to diverse and extreme environments, making it an ideal model for studying plant responses to climate variability. Ecological niche models (ENMs) are powerful tools for simulating species' potential distributions across different time periods, thereby aiding biodiversity conservation. In this study, 75 filtered occurrence records of *C. graciliflora* and 19 climatic variables, derived from field surveys and herbarium records in China, were used to model the species' potential distribution across 6 periods (Last Interglacial, Last Glacial Maximum, Middle Holocene, Current, Future 2050s, and Future 2070s). Research findings indicate that key environmental factors influencing its distribution include mean diurnal temperature range (bio2), mean temperature of the warmest quarter (bio10), annual precipitation (bio12), and precipitation of the driest month (bio14). Historically, suitable habitats for *C. graciliflora* were primarily concentrated south of the Qinling-Huaihe River region, closely associated with the Qinling, Luoxiao, Nanling, and Mount Wuyi ranges. During the Last Glacial Maximum, extensive suitable habitats existed in southwestern China, subsequently contracting to refugia in the Qinling and Mount Wuyi areas, underscoring these regions as refugia for *C. graciliflora*. Future projections indicate an overall decline in suitable habitat, highlighting the significant impacts of global warming on its long-term survival. Notably, this study represents the first application of the MaxEnt model to infer historical refugia of *C. graciliflora* while simultaneously integrating analyses of its future distribution shifts. This work fills the gap in long-term climate response research for this species and evaluates the impacts of climate change on its distribution, providing valuable insights for its phylogeography and conservation practice. By further identifying core habitats and clarifying their climate sensitivity, the findings provide a basis for developing targeted conservation strategies that prioritize key ecological areas and mitigate the risk of habitat loss.

Key words: Climate change, geographical distribution, MaxEnt model

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Introduction

Evidence is mounting that the distribution patterns of species are influenced by rapid temperature changes, including shifts in temperature, precipitation, and other climatic factors (Corlett and Westcott 2013; Du et al. 2024; Zhu et al. 2024). In particular, decreases in temperature typically cause species to retreat to lower latitudes and altitudes, whereas warming promotes expansion toward higher latitudes and altitudes (Spence and Tingley 2020). During the Last Glacial Maximum (LGM), the high-altitude mountains of the Qinghai–Tibet Plateau acted as a barrier to the eastward expansion of high-latitude glaciers in Asia (Deng and Ding 2015; Zhou et al. 2017). This allowed many high-altitude regions in China, including the Qinghai–Tibet Plateau, Daba Mountains, Wushan Mountains, Dalou Mountains, Wuling Mountains, Shennongjia Forestry District, Nanling Mountains, Mount Wuyi, and the mountains of Taiwan, to serve as glacial refugia for plants (Chen et al. 2011). During this period, species either migrated to refugia or evolved *in situ* through genetic variation to cope with temperature fluctuations. However, if migration or adaptation could not keep up with climate change, species would face population decline, range contraction, or extinction (Webb 1997; Wiens and Graham 2005). Furthermore, human activities have exacerbated habitat fragmentation, posing increasing threats to plant diversity. As these impacts intensify, understanding both the historical and potential future distributions of endangered species is critical for biodiversity conservation.

Ecological niche models (ENMs) are powerful tools for predicting species distributions based on known occurrence records and environmental variables. These predictions are generated through algorithmic modeling and can be projected across different temporal and spatial scales (Araújo and Peterson 2012). The model can be applied to simulate the potential range of species under different periods and climatic conditions, which is crucial for understanding how species respond to diverse climatic conditions. Currently, commonly used ENMs include GARP (Elith et al. 2006), BIOCLIM (Nix 1986), DOMAIN (Carpenter et al. 1993), and the MaxEnt model (Phillips and Dudík 2008; Elith et al. 2011; Liu et al. 2021). Among them, the MaxEnt model (i.e., maximum entropy model) is widely used for predicting plant and animal distributions. It is favored for its fast processing, high accuracy, and ability to perform well with limited distribution data compared to other models (Kaky et al. 2020; Liu et al. 2021; Zhang et al. 2021a). *C. graciliflora*, a perennial herb, belongs to the genus *Calanthe* in the Orchidaceae (subfam. Epidendroideae). It is one of the most widely distributed species of the genus *Calanthe*, with the broadest latitudinal range and the greatest cold tolerance. It is primarily distributed in subtropical montane forests of China, mainly in the Qinling Mountains, Daba Mountains, Luoxiao Mountains, Nanling Mountains, and Mount Wuyi, all of which fall within the subtropical monsoon zone, where precipitation is abundant yet strongly seasonal (Clayton and Cribb 2013). These regions are characterized by evergreen broad-leaved forests at elevations of 600–1500 m and mixed coniferous–broadleaf forests at 1500–2500 m. The high humidity (>75%), acidic, humus-rich soils (pH 5.0–6.5), and shaded understories provide optimal microhabitats for the species (Chen et al. 1999).

The species is believed to have originated on the Asian continent and is endemic to China, diverging from its ancestor in the early Pleistocene (2.5 Ma) (Chen 2020). However, the changes in its geographical distribution from the Pleistocene

to projected conditions in the 2070s, as well as the location of its potential glacial refugia in China, remain unclear. Furthermore, sympatric distribution, overlapping flowering periods, and hybridization between *C. graciliflora* and closely related species play key roles in maintaining species diversity and stabilizing forest ecosystems (Carpenter et al. 1993). *C. graciliflora* is also valued for its colorful flowers and its medicinal properties, making it highly sought after for ornamental and medicinal use. Nevertheless, human activities, combined with habitat loss and climate change, have led to significant annual declines in its natural populations. Ongoing mountain development has particularly contributed to habitat loss, causing localized population extinctions in southeastern China (Qiu et al. 2023). Currently, the species is listed as a near threatened (NT) species by the International Union for Conservation of Nature (IUCN). It is also included under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), with international trade strictly prohibited and regulated. Although *C. graciliflora* has a broad geographic range, it is highly sensitive to microenvironmental changes and exhibits specific ecological niche preferences, making it a potential indicator species for assessing the impacts of climate change on montane plants. Therefore, the MaxEnt model was used to predict the potential distribution areas of *C. graciliflora* under 6 periods: Last Interglacial (LIG), Last Glacial Maximum (LGM), Middle Holocene (MH), Current, and Future (2050s, 2070s). The study explored the following two questions: (1) What were the potential refugia of the species during the LGM? (2) How have the spatial distribution patterns and suitable habitat areas of the species shifted from the Pleistocene to projections for the 2070s? This study provides a framework for understanding the phylogeography and guiding the conservation of *C. graciliflora* and other montane orchid species.

Materials and methods

Species distribution data collection

Occurrence records of *C. graciliflora* were mainly obtained from the Chinese Virtual Herbarium (CVH, https://www.cvh.ac.cn/, accessed on 20 July 2022), Global Biodiversity Information Facility (GBIF, https://www.gbif.org/, accessed on 21 July 2022), and Flora of China. A total of 229 latitude and longitude record points for the species were gathered from relevant literature and fieldwork recordings. A 1 km × 1 km buffer zone was established across China using ArcGIS 10.8.1 (ESRI 2020). To reduce spatial bias from clustered sampling, redundant and misidentified records were removed, and only one occurrence point was retained per buffer zone for subsequent ecological niche modeling.

Environmental variable data acquisition

Nineteen bioclimatic factors in six different periods were downloaded from WorldClim (http://www.worldclim.org/), including the Last Interglacial (LIG, 120 ka), Last Glacial Maximum (LGM, 22 ka), Middle Holocene (MH, 6 ka), Current, and Future (the 2050s, 2070s). The spatial resolution was 30". Climate data were obtained from the CCSM4 model developed by the National Center for Atmospheric Research (NCAR) under the framework of the Coupled Model Intercomparison Project Phase 5 (CMIP5). CCSM4 was chosen for its well-doc-

umented performance in simulating global and regional climate processes (Gent et al. 2011) and its demonstrated utility in ecological studies, such as predicting species–community decoupling under climate change (Thomas et al. 2023). The model's high-resolution outputs and reduced biases in critical variables ensured robustness for biogeographical analyses. For future projections in the 2050s and 2070s, the Representative Concentration Pathway (RCP) 2.6 scenario was used. This low-emission pathway aligns with global climate mitigation efforts, provides a conservative estimate of potential climate impacts on species distributions, and allows comparability with recent studies on threatened taxa under optimistic scenarios. Subsequently, the Mask tool in ArcGIS 10.8.1 (ESRI 2020) was used to clip and extract regional climate data in China and then convert them to ASCII format for further analysis.

Environmental variable data screening

Multicollinearity among 19 climatic variables can lead to model overfitting, which affects the evaluation of simulation results (Graham 2003; Zhang et al. 2014). Therefore, environmental factors with a small contribution at $|r| \geq 0.8$ were removed using Pearson correlation analysis. Seven environmental factors were finally identified for model prediction, including mean diurnal range (bio2), isothermality (bio3), minimum temperature of the coldest month (bio6), mean temperature of the wettest quarter (bio8), mean temperature of the warmest quarter (bio10), annual precipitation (bio12), and precipitation of the driest month (bio14). As orchids are highly sensitive to water availability and seasonal drought (Zotz and Bader 2009; Gao et al. 2025), and precipitation has been shown to be a major determinant of orchid distributions (Qiu et al. 2023; Pica et al. 2024; Tsiftsis et al. 2024), bio12 and bio14 were prioritized under collinearity to represent overall water supply and drought stress in the subtropical monsoon regions where *C. graciliflora* occurs.

MaxEnt model building and parameter setting

We collected environmental data and species occurrence points across six time periods, focusing on climate variables that significantly affect species suitability. Climate data for each period were matched with species distribution points. The environmental data (*.asc) and distribution points of *C. graciliflora* (*.csv) were imported into the MaxEnt program for habitat distribution modeling. We randomly selected 75% of the data as the training set and 25% as the test set for model evaluation. To improve methodological rigor and address potential uncertainties in conventional MaxEnt modeling, we complemented the core modeling process with additional evaluations of environmental variable importance and species–environment response curves. Variable contributions were quantified using jackknife tests, while response curves were analyzed to verify the plausibility of adaptive thresholds to key climatic factors. Together, these supplementary analyses allowed for a more robust identification of environmental drivers and reduced biases in model outputs. Model settings included a maximum of 1000 iterations to ensure convergence, with 10 bootstrap replicates to improve stability. The random seed option was applied, and the average output across repli-

cates was used as the final prediction. Model performance was evaluated using the area under the receiver operating characteristic curve (AUC), where values of 0.50–0.60 indicate invalid predictions, 0.60–0.70 poor, 0.70–0.80 fair, 0.80–0.90 good, and 0.90–1.00 excellent (Phillips et al. 2006; Phillips and Dudík 2008).

Division of suitable regions

The MaxEnt model results were imported into ArcGIS 10.8.1 for further analysis. Potential distribution maps for different time periods were classified into suitability categories and then visualized. Based on the model's equal training sensitivity and specificity thresholds, fitness zones were categorized into four levels: unsuitability, low suitability, moderate suitability, and high suitability. Potential distribution areas with different suitability levels were obtained through area tabulation using the SDMtoolbox in ArcGIS 10.8.1 (ESRI 2020).

Results

Overview of verified distribution records

A total of 75 occurrence records were retained after spatial filtering and data validation and were used for subsequent ecological niche modeling (Fig. 1). These occurrence points are broadly distributed across the montane regions of central, eastern, and southern China, particularly in Sichuan, Hunan, Jiangxi, Zhejiang, Fujian, Guangdong, and Guangxi provinces. The validated distribution records span a wide range of latitudes and elevations in central and southern China, with notable concentrations in subtropical mountainous areas.

Screening for dominant environmental factors

The environmental variables used in the MaxEnt model were selected based on their ecological relevance to *C. graciliflora* and their availability in the WorldClim database (Manthey and Box 2007; Fick and Hijmans 2017; Sun et al. 2020). Nineteen bioclimatic variables from the WorldClim dataset were initially assessed, and highly collinear predictors ($|r| > 0.8$) were excluded based on Pearson correlation analysis. Ecologically relevant variables, particularly precipitation-related factors, were prioritized due to the species' association with distinct dry and wet seasons. The results of the effects of environmental factors on species distribution in the MaxEnt model showed that the largest contribution rate was the precipitation of the driest month (bio14). This was followed by bio12, bio10, and bio2 (Table 1). The cumulative contribution of these four factors accounted for 92%. These findings indicate that the distribution of *C. graciliflora* is strongly influenced by these environmental conditions.

The results of the variable-importance jackknife test showed relatively high gain values for bio2 and bio12 when only variables were used (Fig. 2). This indicated that these environmental factors contributed more strongly to the distribution of *C. graciliflora*. When a single variable was ignored, bio10 showed the greatest drop in model gain, implying that this variable contained information that other variables did not.

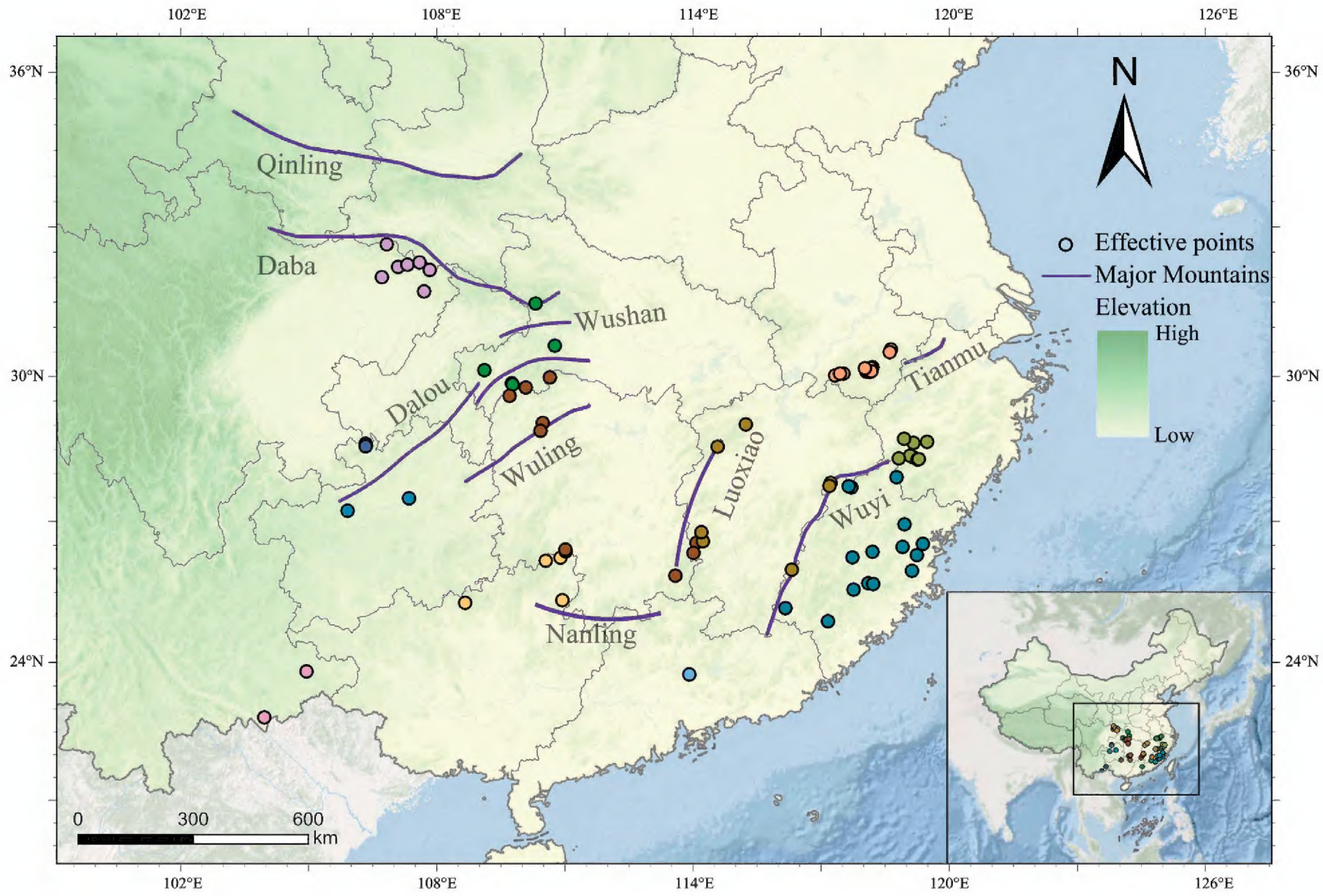

Figure 1. Geospatial distribution of effective occurrence records of *C. graciliflora*. Note: The color of each effective point indicates the province where it is located, and the purple lines indicate major mountains mapped using the Digital Mountain Map of China (Nan et al. 2022).

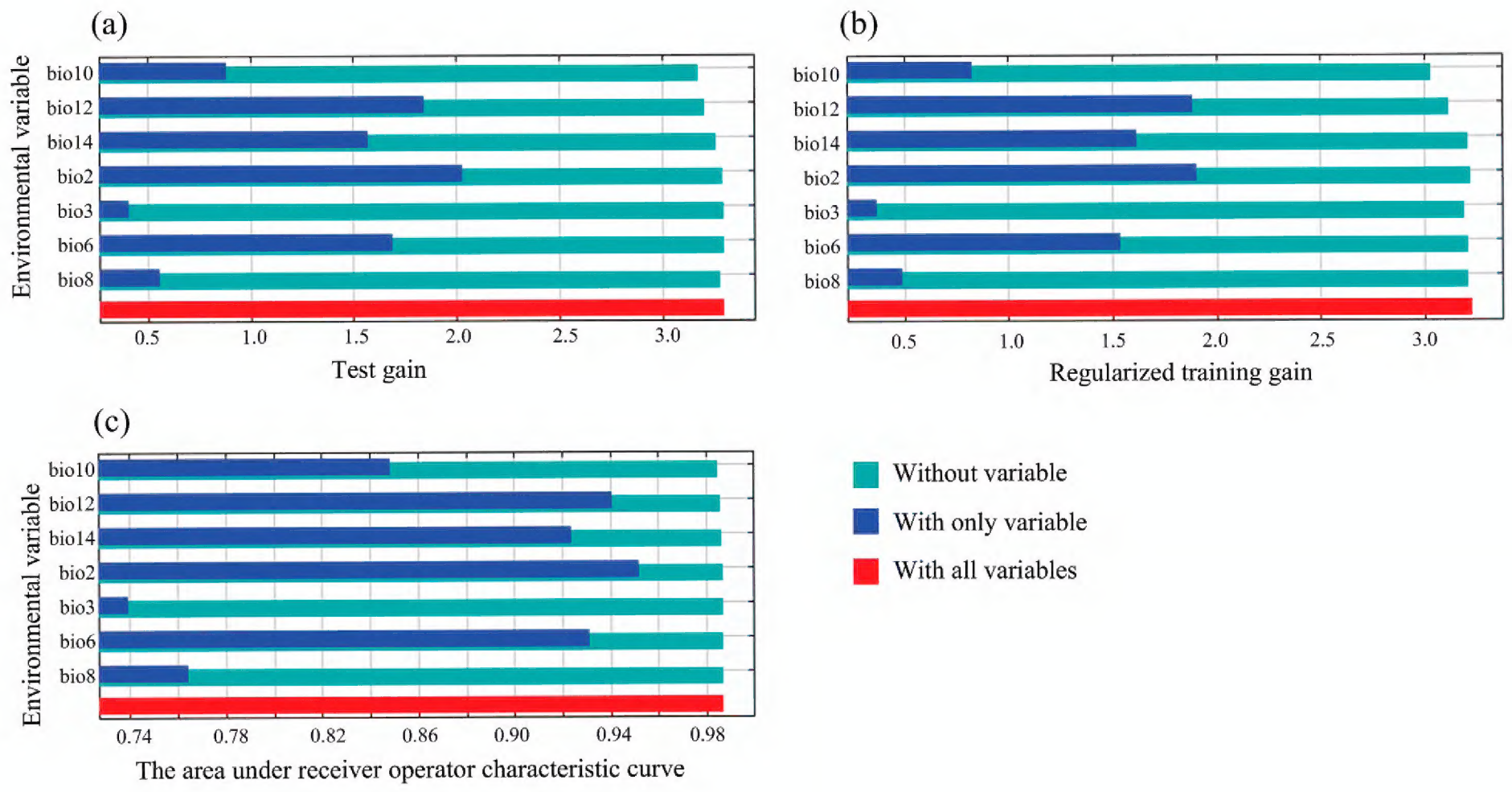

Figure 2. Impact of bioclimatic variables on the predictive performance of *C. graciliflora* distribution.

Table 1. Contribution rate of seven bioclimatic variables to *C. graciliflora* distribution based on the MaxEnt model.

Symbol	Environment variable	Percent of contribution
bio14	Precipitation of the driest month (mm)	30.6
bio12	Annual precipitation (mm)	27.0
bio10	The mean temperature of the warmest quarter (°C)	25.9
bio2	Mean diurnal range (°C)	8.5
bio3	Isothermality (bio2/bio7) (×100)	4.6
bio8	The mean temperature of the wettest quarter (°C)	2.4
bio6	Minimum temperature of the coldest month (°C)	1.0

In summary, the environmental factors having significant effects on the geographic distribution of *C. graciliflora* were bio2, bio10, bio12, and bio14. These variables were selected because they represent critical climatic thresholds for plant survival and growth, particularly in subtropical and montane regions where *C. graciliflora* is predominantly found.

The response curve results of the four main climate factors are shown in Fig. 3. When the presence probability was greater than 0.5, the range of response values for the mean diurnal range was 6.3–8 °C, the range for the mean temperature of the warmest quarter was 21.5–25 °C, the range for the annual precipitation was 1,500–2,800 mm, and the range for the precipitation of the driest month was 30–170 mm. These ranges align with the known ecological preferences of *C. graciliflora*, further validating the selection of these variables.

MaxEnt model accuracy testing

The average AUC of the prediction model for the habitat suitability of *C. graciliflora* under current climate conditions was 0.989, with a standard deviation of 0.001. This value markedly exceeded the simulated random prediction distribution value of 0.5, demonstrating high accuracy and reliability of the prediction results (Fig. 4).

Prediction of suitable regions

As shown in Fig. 5, the suitable regions of *C. graciliflora* in six different periods were primarily distributed in the subtropical evergreen broad-leaved forests south of the Qinling–Huaihe line and were closely related to the Hengduan Mountains, Qinling Mountains, Luoxiao Mountains, Nanling Mountains, Mount Wuyi, and Taiwan Mountains. The highly suitable regions were stably distributed in Mount Wuyi and the Luoxiao Mountains. The moderately and poorly suitable regions were mainly concentrated in the Qinling Mountains, Nanling Mountains, and Taiwan Mountains, as well as surrounding the highly suitable regions.

Prediction of suitable regions in the past period

During the LIG (Fig. 5a), the suitable habitats for *C. graciliflora* were primarily distributed across subtropical evergreen broad-leaved forests in the present-day provinces of Chongqing, Yunnan, Guizhou, Hainan, Fujian, and Zhejiang.

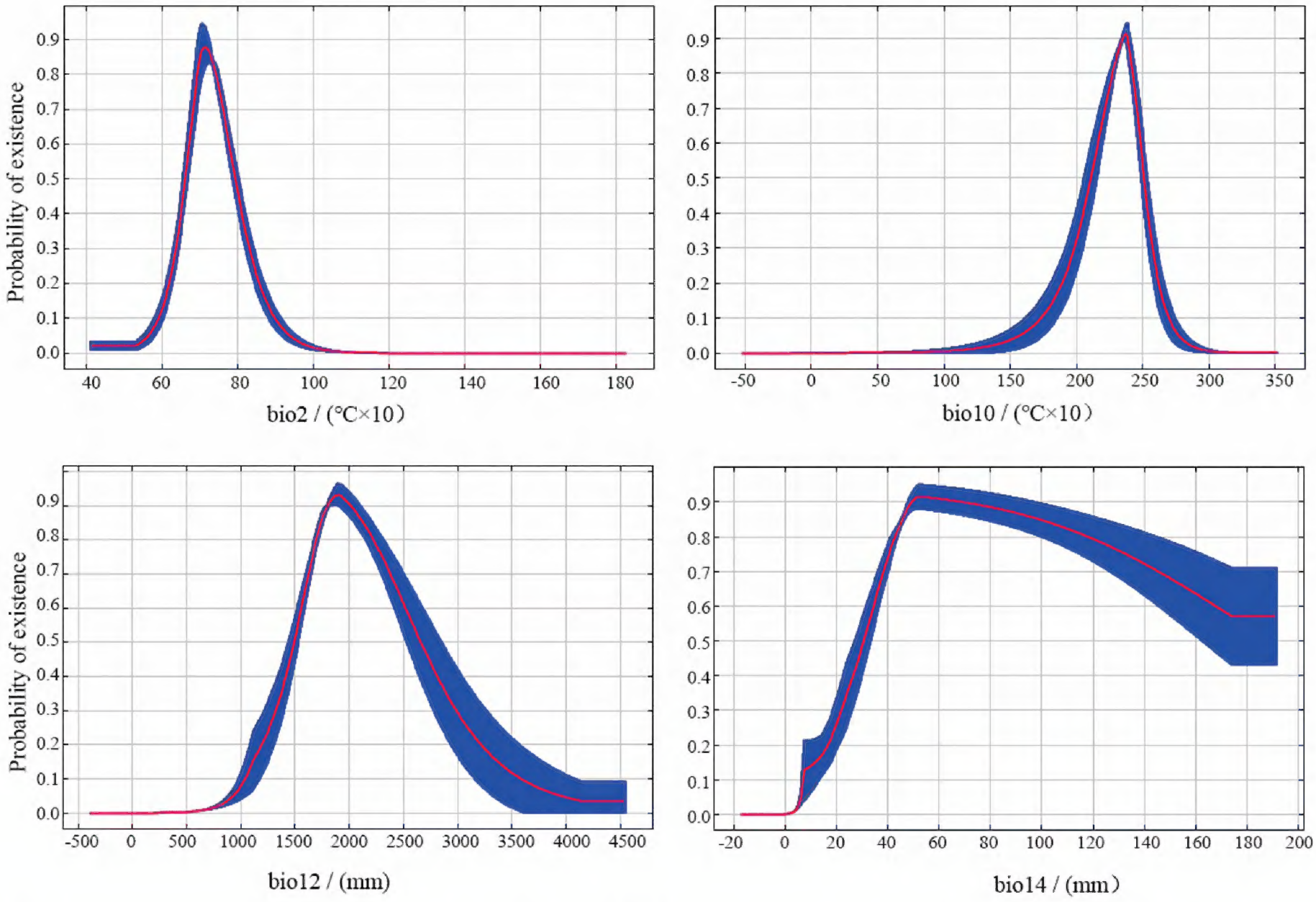

Figure 3. Response curves of *C. graciliflora* presence probability to key environmental variables. Note: The red curves show the average over 10 replicate runs; the blue bands show the standard deviation (SD) calculated over 10 replicates.

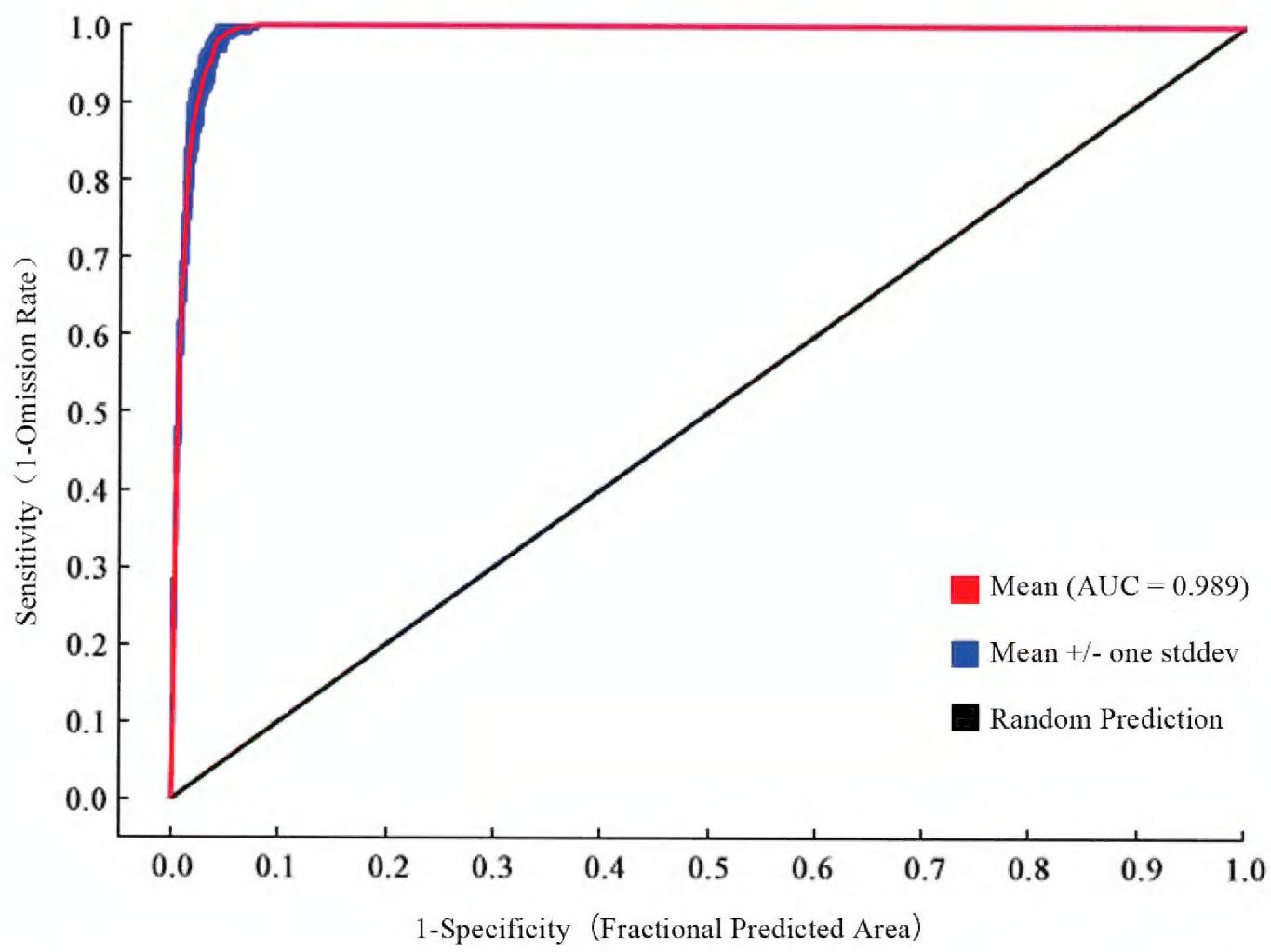

Figure 4. MaxEnt model achieves an outstanding prediction of *C. graciliflora* distribution (AUC = 0.989). Note: AUC values range from 0 to 1, where a value closer to 1 indicates better classifier performance, while a value near 0 suggests poor performance.

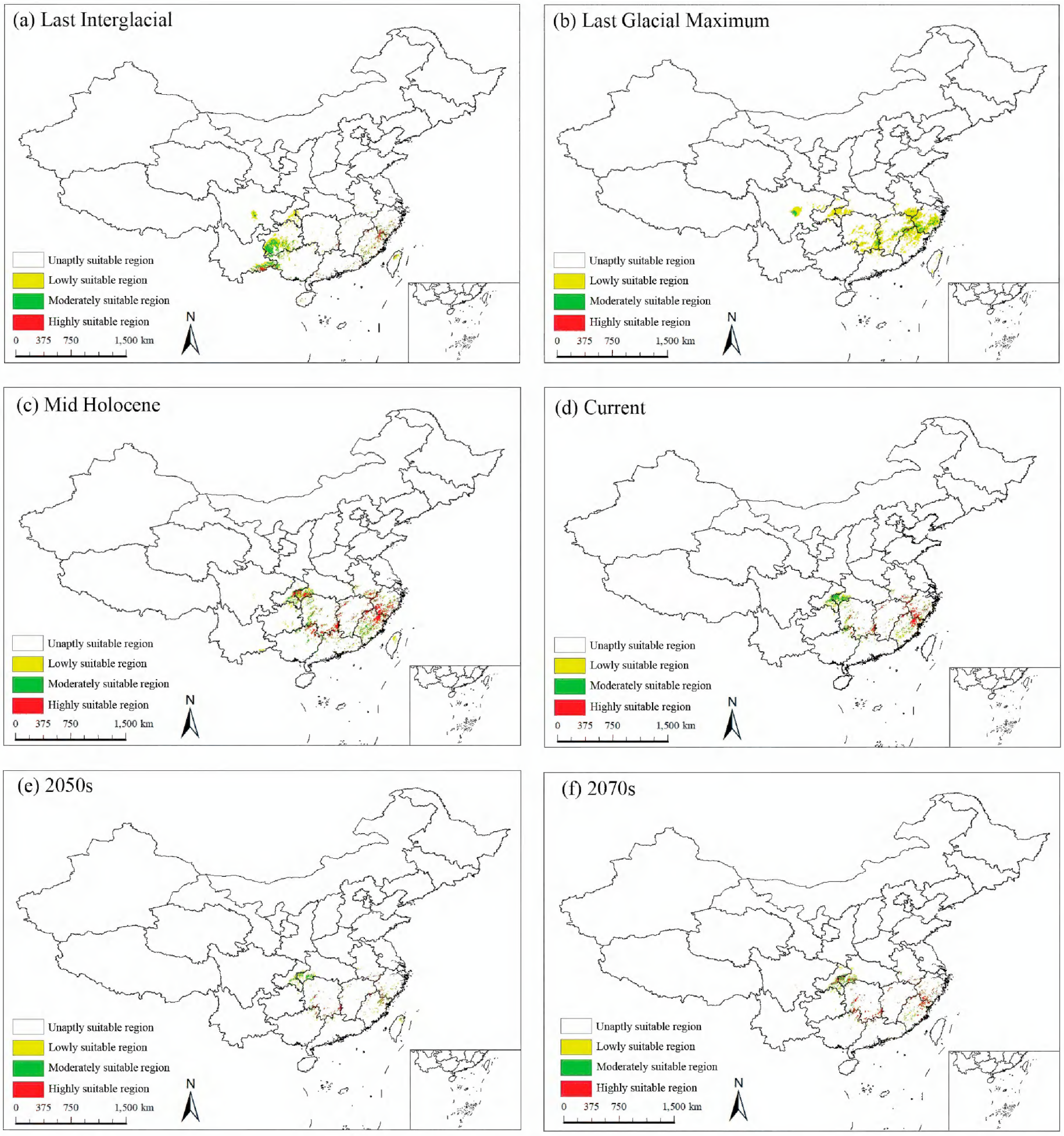

Figure 5. Habitat suitability maps showing the occurrence of *C. graciliflora* in six different periods. Note: **a.** LIG: Extensive suitable regions were present in the southern section of the Hengduan Mountains, exhibiting a discontinuous pattern from west to east; **b.** LGM: The suitable regions in the southern section of the Hengduan Mountains disappeared while expanding into the Qinling Mountains; **c.** MH: The suitable regions were overall similar to the present-day distribution pattern; **d.** Current: The suitable regions are primarily found in central and eastern China; **e.** 2050s: The distribution range of suitable regions will generally shrink; **f.** 2070s: The overall suitable regions increased compared with the previous period, while the highly suitable regions in Taiwan disappeared.

These regions exhibited a discontinuous distribution from west to east, closely linked to the Hengduan Mountains, Mount Wuyi, and the Taiwan Mountains. Notably, a wide range of suitable regions was present in the southern section of the Hengduan Mountains during this period. However, during the LGM, the suitable regions in the southern Hengduan Mountains disappeared (Fig. 5b), while suitable regions expanded to the Qinling Mountains, Luoxiao Mountains,

and Mount Wuyi. These findings suggest that the climatic conditions during the LGM had a significant impact on the geographic distribution of *C. graciliflora*. The Qinling Mountains, Luoxiao Mountains, and Mount Wuyi likely served as refugia for the species during this period. During the MH (Fig. 5c), the suitable areas largely resembled the present-day distribution pattern. Highly suitable regions were primarily concentrated at the border of Chongqing and Hubei, as well as in southern Hunan, Fujian, Zhejiang, and Taiwan. These habitats formed a linear distribution along mountain ranges, highlighting the species' dependence on specific climatic and ecological conditions.

Prediction of suitable regions in the present period

As shown in Fig. 5d, the suitable regions of *C. graciliflora* are primarily found in central and eastern China, aligning well with their MH distribution areas. The core distribution area corresponds closely with the recorded distribution points of the species. Additionally, the predicted potential distribution area extends beyond the observed occurrences. The highly suitable regions were mainly distributed in the subtropical evergreen broad-leaved forest zones, particularly in the Jiangxi–Hunan border region, and the Fujian and Zhejiang provinces. These areas are associated with the Luoxiao Mountains and Mount Wuyi, which are characterized by montane forests and rich biodiversity, providing ideal habitats for *C. graciliflora*.

Prediction of suitable regions in future periods

In the future, in the 2050s and 2070s, the distribution range of suitable regions for *C. graciliflora* is projected to shrink overall. Notably, a highly suitable region is predicted to emerge in the high-altitude areas of Taiwan by the 2050s. However, this suitable habitat is expected to disappear by the 2070s. These findings suggest that global warming may affect species growth, leading populations to migrate to higher altitudes.

Estimation of suitable area

Predictions indicate that the total area of suitable regions for *C. graciliflora* shows a decreasing trend under different climatic conditions from the past to the future (Table 2). During the LIG, suitable regions covered a total area of 12.377×10^4 km^2, or 1.279% of the country's geographical area. Of this, 1.660×10^4 km^2 represented the highly suitable area, accounting for 0.172% of the country's total land area. During the LGM, the area of suitable regions decreased significantly. In the MH, suitable regions covered 15.728×10^4 km^2, or 1.626% of the national land area. Among these, the areas of the moderately and highly suitable regions were the largest among the six periods, accounting for 0.537% and 0.600% of the national land area, respectively. During the present period, the total suitable habitat area for the species is approximately 9.808×10^4 km^2, representing 1.014% of the national land area. Compared with the MH, this area shows a decreasing trend. In the future 2050s and 2070s, the total area of suitable regions will decrease by 5.122×10^4 km^2 and 2.868×10^4 km^2, respectively, compared with the present period. The current highly suitable region for

Table 2. Predicted suitable regions for *C. graciliflora* in China across time (× 10^4 km^2).

Periods	Unsuitable region	Lowly suitable region	Moderately suitable region	Highly suitable region	Total suitable region
LIG	955.123	6.305	4.412	1.660	12.377
LGM	946.617	18.068	2.672	0.144	20.883
MH	951.772	4.731	5.193	5.804	15.728
Current	957.692	3.371	3.515	2.922	9.808
2050s	962.814	1.777	1.739	1.170	4.686
2070s	960.560	2.126	2.223	2.591	6.940

C. graciliflora spans 2.922 × 10^4 km^2. However, projections suggest a 59.9% reduction (to 1.170 × 10^4 km^2) by the 2050s, followed by a partial recovery to 2.591 × 10^4 km^2 in the 2070s. This pattern reflects its historical resilience to climate fluctuations. This pattern reflects the historical resilience of *C. graciliflora* to climate fluctuations. The initial decline is likely due to rapid warming (>2 °C), which disrupts the fog–shade equilibrium in core habitats and reduces high-suitability areas. The subsequent recovery may result from elevational migration, as warming pushes subtropical forests upward, creating new suitable zones similar to its MH distribution. This bimodal "decline followed by recovery" pattern mirrors its survival through past climatic upheavals, underscoring the critical role of mountainous refugia in its long-term persistence.

Discussion

Environmental factors acting on organisms include abiotic and biotic factors (Hamby et al. 2016). Recent studies have shown that among abiotic factors, precipitation and light play direct roles in the geographical distribution of orchids (Zhu et al. 2014). The results of this study showed that the factors affecting the geographical distribution of *C. graciliflora* were temperature-related factors (bio2, bio10) and precipitation factors (bio12, bio14). Therefore, this study is consistent with previous research. Additionally, other studies found that the geographical distributions of *Paphiopedilum micranthum* (Zhang et al. 2021b) and *Bletilla striata* (Luo et al. 2025) were significantly affected by precipitation and temperature. The species richness of wild orchids in Xishuangbanna, China, showed a monotonically decreasing relationship along the gradient of average annual land surface temperature (Yu et al. 2016).

Organisms have limits to the range of environmental conditions they can adapt to. When these limits are exceeded, they may experience negative effects on growth, development, and reproduction, or even face mortality (Shelford 1931; Erofeeva 2021). In the MaxEnt niche model, the response curves of environmental factors illustrate the relationship between species' occurrence probability and environmental conditions. It is generally accepted that when the occurrence probability exceeds 0.5, the corresponding environmental factors are favorable for the survival and expansion of the target species (Dong et al. 2020; Wang et al. 2020). The response curve results of this study showed that when the probability was greater than 0.5, the annual precipitation response value was 1,500–2,800 mm, the precipitation of the driest month response value was 30–170 mm, the mean diurnal range response value was 6.3–8 °C, and

the mean temperature of the warmest quarter response value was 21.5–25 °C. The results indicated that this range of environmental factors represents the limit of normal growth for *C. graciliflora*.

In Quaternary climatic events, there may be two evolutionary patterns of species: migration to glacial refugia or *in situ* evolution in refugia (Fan et al. 2016; Liang et al. 2017; Ye et al. 2017). Xiao et al. (2021) simulated the niche of *Phoebium bournei* and found that the plant groups exhibited a model of *in situ* evolution in refugia in response to climate change. Their distribution areas demonstrated a trend of recurrent contraction and expansion from the past to the future. Li et al. (2021) found that *Fraxinus chinensis* may have followed a refugial migration model in response to the climate during the LGM. During this period, the species migrated to the mid-subtropical evergreen broad-leaved forest zone (Wushan Mountains), which was presumed to be a refugium for the species. The results of this study indicated that *C. graciliflora* may also have followed two models of climate response in Quaternary climatic events: migration to glacial refugia and *in situ* evolution in refugia. During the LGM, extensive suitable habitats in the subalpine coniferous forest zone (Hengduan Mountains) disappeared, while suitable regions emerged in the northern subtropical evergreen–deciduous broad-leaved mixed forest zone (Qinling Mountains). This suggests that the northern subtropical transitional forests may have served as glacial refugia for the species, which may have adopted a migratory response to adapt to environmental changes. The core location of the suitable zone in the mid-subtropical evergreen broad-leaved forest zone (Mount Wuyi) has consistently persisted throughout Quaternary climatic events. This suggests that the species may also have adopted a model of *in situ* evolution in refugia, adapting to changing environments through genetic variation or phenotypic plasticity.

Global warming events significantly impact species distribution, causing suitable distribution areas to shrink and expand toward higher latitudes and altitudes (Hallam and Wignall 1997; Bell and Gonzalez 2009; Salamin et al. 2010; Huntley et al. 2013). Khwarahm et al. (2021) found that the habitat ranges of *Salamandra infraimmaculata* and *Neurergus derjugini* in Iraq would shrink by 3.42% and 4.16%, respectively, by the 2070s due to global warming. Projections indicate that the climatically suitable area for *C. graciliflora* will decrease by approximately 52% by the 2050s and by 29% by the 2070s compared with current conditions. Although its projected extent of occurrence (EOO) and area of occupancy (AOO) remain above the IUCN's Endangered thresholds, the magnitude of decline, combined with ongoing anthropogenic disturbance and habitat fragmentation (Li et al. 2022), warrants consideration in reassessing its threat status. Incorporating climate change vulnerability into Red List evaluations is therefore essential to strengthen conservation prioritization (Mancini et al. 2024).

The observed response patterns of *C. graciliflora* are consistent with other montane orchids. Evans et al. (2020) projected range contraction and upslope or poleward shifts for *Orchis simia* and *O. purpurea*, while Pica et al. (2024) predicted habitat losses exceeding 90% for *Cephalanthera rubra*, *Epipactis microphylla*, and *Limodorum abortivum*. In contrast, some *Habenaria* species appear to exhibit range expansion under warming scenarios (Qiu et al. 2023). These interspecific differences likely reflect variation in functional traits, such as the presence of underground storage organs or evergreen versus deciduous habits,

as well as niche breadth and adaptive capacity, underscoring the importance of cross-species comparisons for informing targeted conservation strategies.

Continuous attention should be given to the conservation of wild germplasm resources through a combination of *in situ* and *ex situ* strategies. Based on occurrence data and model projections, *in situ* protection should prioritize the regions south of the Qinling–Huaihe line, including montane forests at 800–1,200 m in the Nanling Mountains and 1,200–1,600 m in Mount Wuyi. These core zones can be integrated into existing or planned national park systems to ensure long-term species persistence. For newly identified climatically suitable areas projected in the future, such as Taiwan, small-scale protected zones should be strategically established to facilitate species migration and mitigate human impacts. *Ex situ* measures, including seed banking, cultivation in botanical gardens, and assisted reproduction, are recommended where natural habitats are projected to decline. Given the species' low seed set and germination rates (Shefferson et al. 2020), these interventions are crucial for maintaining population stability. Furthermore, climatic conditions during the MH provide valuable guidance for reintroduction or planting programs in areas with similar current or projected conditions, supporting population recovery and ecological restoration.

A key limitation of this study is that it focuses solely on the influence of bioclimatic variables on species distribution. However, suitable regions for species are influenced by various factors, including climate and topography as abiotic factors, alongside biological factors such as competition. Consequently, relying solely on methods like jackknife importance testing to identify dominant variables may lead to predictive inaccuracies. Furthermore, the inherent lag in plant responses to climate change can exacerbate discrepancies between modeled projections and future distributions. Looking ahead, advances in high-resolution environmental datasets, modeling techniques, and field monitoring will allow more accurate assessments of the drivers shaping species distributions. The rapid development of machine learning provides additional opportunities to integrate diverse algorithms, such as Random Forest, Support Vector Machines, and Gradient Boosting, with multi-source environmental data. This integration can facilitate multi-factor habitat suitability assessments and inform more targeted conservation measures. Importantly, *C. graciliflora* has not previously been the subject of comprehensive climate-driven distribution modeling, making this study an important baseline for future research on *Calanthe* and other terrestrial orchids. Additionally, species within the genus *Calanthe* often exhibit overlapping ecological niches, suggesting that genus-level analyses could provide a more integrated understanding of climate change impacts and support systematic conservation planning.

Conclusion

In conclusion, during the Quaternary glacial–interglacial cycle, *C. graciliflora* adopted both migration and *in situ* evolution models within refugia in response to climate change. The Qinling Mountains and Mount Wuyi are suggested as potential refugia for this species during the LGM. Additionally, this study analyzed climate change scenarios for the future 2050s and 2070s using RCP2.6, which represents an optimistic carbon emission trajectory. However, controlling real-world emissions remains a challenge. To develop effective conservation strategies for *C. graciliflora* in the future, modeling and forecasting the species'

ecological niche under diverse climate change scenarios is recommended. Furthermore, the study identifies the Qinling Mountains and Mount Wuyi as suitable and stable distribution areas, supporting their designation as conservation zones for the species. However, the genetic structure and diversity of *C. graciliflora* populations in these regions remain poorly understood. Therefore, conducting population genetic studies is recommended to provide a robust theoretical foundation for conservation efforts.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Conceptualization: AL, CH, JZ, WH. Environmental data: PG, AL. Statistical analysis: AL, LC, JZ. Visualization: JZ, ML, SW. Model evaluation and validation: CH, AL. Writing – original draft: PG, AL, LC, JZ. Writing – review and editing: PG, AL, LC, SW, CH, ML, JZ, WH. All authors contributed to the final version of the manuscript and approved the submitted version.

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Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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